

The University of Chicago

STRUCTURE OF SEEDLIKE FRUCTI-
FICATIONS FOUND IN COAL BALLS
FROM HARRISBURG, ILLINOIS

A PART OF A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF BIOLOGICAL
SCIENCES IN CANDIDACY FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

By
HARRIETTE VALETTA KRICK

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STRUCTURE OF SEEDLIKE FRUCTIFICATIONS
FOUND IN COAL BALLS FROM HARRIS-
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CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 431

HARRIETTE VALLETTA KRICK

(WITH TWENTY-ONE FIGURES)

Introduction

The attention of English and French paleobotanists was early directed to the study of certain seedlike fossils, occurring in the form of impressions and casts in the shales above the coal seams, and as petrifications (coal balls) in the coal seams themselves. LINDLEY and HUTTON (20) ascribed the 3-angled *Trigonocarpum* to palmlike plants similar to the Chilian *Micrococcos*. BRONGNIART (12, 13) and WILLIAMSON (42), studying the cellular anatomy, found a similarity between the structure of the Paleozoic seeds and the seeds of cycads and *Ginkgo* of the present day flora. On the basis of anatomical investigation not concerned with the organs of reproduction, POTONIÉ (30) applied the name Cycadofilices to the group of fossil plants showing characteristics common to pteridophytes and gymnosperms.

In 1903, when OLIVER and SCOTT (29) announced that a certain characteristic seed, *Lagenostoma*, belonged to the fernlike fronds of *Lyginodendron oldhamium*, the name Pteridosperms was proposed for that group of Cycadofilices which bore seeds. Further research proved the two terms to be almost coextensive, so that by many they have come to be used as synonyms (36). Many of the flattened seeds were established, through the researches of GRAND'EURY (14, 15), RENAULT (32), BERTRAND (11), and ARBER (1), as the fructifications of Cordaitales. From a similar study (34, 35), *Lepidocarpum* was recognized as a seedlike reproductive organ of *Lepidodendron*, not included in the Pteridosperms of SCOTT. Between the years 1903-1916, additional work by BERTRAND (4-9), OLIVER (26-28), SCOTT (37), and their pupils greatly increased our knowledge of the structure of these seeds, but very few cases have been found of

continuity of reproductive and vegetative structure, so that actual identity could be established beyond all doubt.

SEWARD (38) classifies the 29 genera so far discovered into three main groups upon the basis of structure: (1) Lagenostomales, radially symmetrical, with integument and nucellus undiverged as in modern cycads; (2) Trigonocarpales, radially symmetrical, with integument and nucellus completely diverged except at the chalazal disk; and (3) Cardiocarpales, with the seeds more or less flattened in cross-section. A broader terminology (24) designates the first two as Radiospermeae, the latter as Platyspermeae. During this time little work was done in America on the structure of such fructifications, and nothing was done in the study of the petrifications.

At about the time that BRONGNIART and WILLIAMSON were working, NEWBERRY (22) published a description of seeds found in coal beds of Ohio. In his discussion of the subject, based upon observation of casts and impressions, he states that *Trigonocarpon* is a nut of a drupaceous fruit, probably belonging to *Sigillaria*. Clearly he thought of these as fruits rather than seeds. He records "detached portions of the external skin or coating bearing the impression of the stem at the base, of the flower above. The latter is sometimes a six-rayed star, such as we might suppose would be left by the fall of a six-parted flower."

LESQUEREUX (19) catalogued species of *Trigonocarpus*, *Cardiocarpus*, and *Rhabdocarpus* from the coal fields of Pennsylvania, Ohio, Illinois, and various other localities in the United States. He admits that the impressions are poor bases for determining the true character of the seed. His terminology is disconcerting: he speaks of the outside layers of the seed as being "composed of various superposed layers, sarcotesta, pericarp, and endocarp." He indiscriminately designates the fossils as nuts, fruits, and seeds. WHITE (39, 40) reported large seeds from Missouri and later made an extensive report on seeds found upon the fronds of *Aneimites* (*Adiantites*) from West Virginia. NOÉ (23) found several genera in northern Illinois.

With the finding of similar vegetative structures in the Coal Measures of America and Europe (17, 31), it seemed worth while to investigate the petrified material for an anatomical study of seed-like structures in the coal balls of America. With this idea in mind, the writer undertook the minute observation of the coal balls which

were brought into this laboratory by Dr. NOÉ. The findings resolved themselves into three points of major interest: (1) a study of serial sections for the identification of the seedlike fructifications from Harrisburg; (2) a morphological interpretation of the material identified; and (3) an environmental theory for a closer correlation between casts, impressions, and petrified material.

Methods and material

The materials used as a basis for this study were from coal balls gathered from coal no. 5 of the O'Gara Mine at Harrisburg, Illinois. Systematic cutting of the coal balls resulted in serial sections 15×10 cm., varying from 2 to 5 mm. in thickness. From these sections thin slides suitable for use in microscopic study were prepared, following two general methods.

I. The older method consisted in grinding the thick sections with carborundum powder on a rotating metal disk or on a glass plate. This took many hours of labor and some skill to obtain the proper uniform thinness. It is obvious that in this process entire seeds of small diameter could be entirely overlooked unless careful watch was constantly maintained. The loss which was incurred through the cut of the saw and the subsequent grinding often left little clue for identification. Of the seeds dealt with in this paper, the larger longitudinal sections of *Trigonocarpon parkinsoni* were prepared successfully in this way, as were also several sections of *T. pusillus* and *Lepidocarpon lomaxi*, which were imbedded in a softer matrix which cracked readily. From these, celloidin films could not be taken because the solvent used dissolved the mounting medium.

II. The celloidin film method was devised by KOOPMANS in collaboration with WALTON (18) in 1928, and is now being used by LECLERQ, GORDON, HEMMINGWAY, and others with satisfactory results. In its simplest terms it involves the following steps:

1. Smooth the surface with carborundum powder of medium grain.
2. Wash thoroughly in running water to remove all particles of carborundum.
3. Etch with acid (hydrochloric acid for calcareous material; hydrofluoric acid for siliceous material). Varying strengths of acid were found to be necessary, according to the composition and con-

sistency of the coal ball. GORDON and HEMMINGWAY recommend a very dilute acid for only a very few seconds. In this laboratory it was found that when considerable pyrite was present, a 10 per cent solution acting for 1-2 minutes was not any too strong to give a desirable etching depth, while in other instances a 5 per cent solution acting for just a few seconds was sufficient. When several cuts from the same coal ball were to be etched, time and material were saved by pouring the acid over the specimens in a shallow tray, as for developing plates, and gently rocking the tray until the desired degree of etching had been obtained. A similar tray was also used for the next step.

4. Wash in gently flowing water to remove all acid, taking care to preserve the organic particles intact.

5. Dry in an oven or open place undisturbed by dust particles. This leaves the bits of carbonaceous material free to be imbedded by the celloidin film.

6. Pour on the solvent to dehydrate and remove all air bubbles.

7. At once pour on the cellulose solution. The European workers use for this a solution of cellulose in amyl acetate or acetone, but here celloidin in ether-alcohol, as suggested by PETRY, was found to be much more effective. Solutions of 4-6 per cent were used.

8. When dry, and before the film begins to wrinkle away from the surface, it can be peeled off and placed between two glass plates in order to maintain a smooth surface. It may be mounted immediately in balsam or it may be used as it is.

The advantages of this later method are obvious, in taking much less time, in obtaining many more sections, and in reducing the waste and uncertainty which is encountered in the making of serial sections by the old method.

To complete the study, reconstructions were made following the method outlined by SALISBURY (33).

Harrisburg seeds¹

A survey of the genera found in the Harrisburg coal balls thus far does not present a great variety when compared with the number

¹ Use of the term seed usually implies not only the permanent retention of the megaspore within the megasporangium, but, that which is more essential, the presence

given by SEWARD (38). From the coal balls of Harrisburg so far cut, four genera, represented by five species, have been identified. Of these, one, *Lepidocarpon*, belongs to a plant whose sole survivors today are classed among the spore-producing pteridophytes. The remainder are truly gymnospermous in character. It is well to keep in mind, however, that this collection deals with coal balls from a single locality, whereas the one mentioned by SEWARD consists of a composite report from many localities.

Lepidocarpon lomaxi Scott.—Of all the seedlike fructifications found in the Pennsylvanian, *Lepidocarpon* represents the most unique. It is one of the most easily recognized seeds in our coal balls, as well as the most abundant.² Essentially it consists of an elongated sporangium borne on the adaxial surface of the pedicel of a lycopodaceous sporophyll. These sporophylls are borne in cones much like *Lepidostrobus*, but all of the specimens so far found are not attached to the original axis.

The sporangia are usually more massive than in the male cones of a similar nature, although the structure of the sporophyll is essentially the same in the very young condition. Later, however, the free edges of the pedicel appear to grow upward as a delayed lamina, leaf-like in character, which completely surrounds the sporangium except for a longitudinal slit along the upper face. In tangential section, as shown in fig. 1, such a structure bears close resemblance to a gymnosperm seed, with a massive nucellus, the leafy lateral emergences of the pedicel appearing as an integument, the slit along the upper side as a micropyle. It was such a section that WILLIAMSON (42) describes as *Cardiocarpon anomalum*.

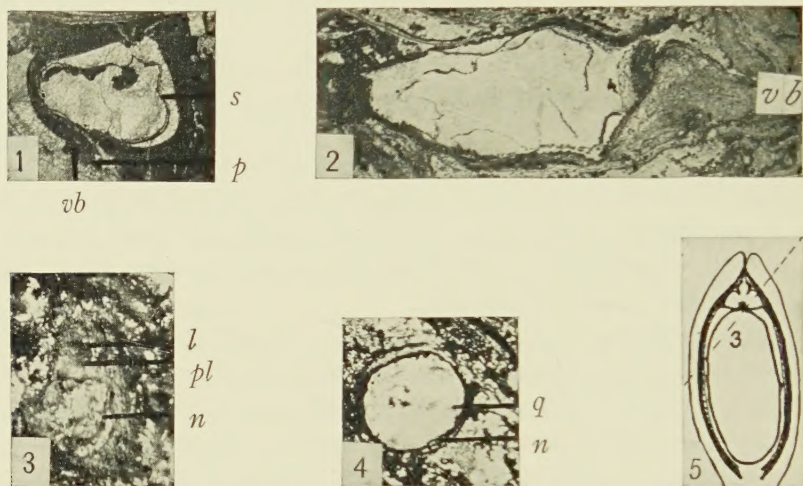
Parallel to the sporophyll pedicel, as seen in fig. 2, the sporangium is 8–10 mm. in length. At the proximal end of the pedicel the sporangium is less than 2 mm. in cross-section, reaching 5 mm. at the distal

of an embryo with its stored food. In the absence of embryos in the Paleozoic, structures with a thinner megaspore membrane, inclosed by a massive nucellus and surrounded by an integument, have been called seeds. To conform with the English and French descriptions, such use of this term has been retained in this paper.

² Besides the material mentioned in this paper, Dr. FREDDA D. REED has found specimens of *Lepidocarpon* in coal balls from Harrisburg and Indiana. Miss INEZ CLARK also reports it from Harrisburg coal balls with which she was working. I have found it in material from Danville, Illinois.

end. In height it varies from 5 to 8 mm. above the surface of the sporophyll. These measurements approximate the range of size given by SCOTT (35) for *Lepidocarpon lomaxi*.

Closely pressing against the inner face of the sporangium is found the thin megaspore membrane, within which the prothallus has been found in some of the English specimens. The sporangium has never



FIGS. 1-5.—Fig. 1, *Lepidocarpon lomaxi*: tangential view showing similarity in structure to ovule with integument; *s*, sporangium wall with megaspore membrane on inner surface; *p*, pedicel of sporophyll with lateral laminal emergence forming covering of sporangium except for slit at top; *vb*, position of vascular bundle. H 210; $\times 5$. Fig. 2, *L. lomaxi*: section taken obliquely parallel to sporophyll pedicel; upturned lamina of sporophyll seen at larger distal end. H 213; $\times 5$. Fig. 3, *Conostoma oblongum*: oblique longitudinal section from micropylar end; *l*, remains of lagenostome; *pl*, plinth cavity; *n*, nucellus. H 213; $\times 10$. Fig. 4, *C. oblongum*: cross-section through basal portion showing remains of gametophyte tissue within undiverged nucellus and integument (*g*). H 213; $\times 10$. Fig. 5; reconstruction of median longitudinal section of *Conostoma oblongum* from Harrisburg material; $\times 7$.

been found with any indication of a dehiscence slit, and from the nature of the megaspore membrane it is supposed that the single functional megaspore with its prothallus was permanently retained within the megasporangium during development of the young embryo. In such a sense, this has been called a seed by SCOTT (35) and others, although its early development could hardly be recognized as an ovule. Since none of the lycopods of the present day show this

near approach to the seed habit, *Lepidocarpon* is of interest as demonstrating one way in which the seed habit may have originated; although it is not necessarily in the direct evolutionary line of the higher seed plants.

Conostoma oblongum Williamson.—This is a slightly 6-angled seed having an average length of 5 mm. and width of about 2 mm. Its extremely small size limits any extensive study of its structure, both by reason of the small number of sections which may be obtained and the large proportion of body length which is lost in the cut of the saw. Of seven sections obtained from the Harrisburg material, only a single instance was found of a cut made so as to show any of the characteristic micropylar structure, and this, because of the obliquity of the cut, does not show the lagenostome (fig. 3).

As is characteristic of the Lagenostomales, the integument and nucellus are undiverged except for a short distance at the micropylar end. The upper portion of the nucellus, which in the other seeds studied makes up a thickened cellular, more or less elongated nucellar beak, is here a lens-shaped cavity with epidermal layer intact. The term "plinth" has been applied to this peculiar structure by English investigators (28). A remnant of the cellular tissue, which at one time may have completely filled the cavity, is present in only a single cushion-shaped mass near the center of the septum which separates the plinth cavity from the larger megaspore cavity below (fig. 5).

In oblique transverse sections taken near the base, such as the one shown in fig. 4, the integument is composed of two kinds of tissue. The outer is a single layer of palisade cells, with cell contents densely carbonized; the inner is a wider layer of cells more or less sclerotic in nature, elongated in a longitudinal direction. In the preservation the nucellar cells, large and conspicuous, are occasionally still in the original state of lack of divergence from the integument.

Trigonocarpon pusillus Brongniart.—This is a slightly 3-angled, unribbed seed, 12 mm. long and 6 mm. wide, apparently with three distinct layers to the integument. The outer parenchymatous layer is but six or seven cells wide, 0.3–0.6 mm. thick, bounded externally by a thick-celled epidermal layer. Mucilage or resin canals, schizogenous in nature, are numerous in this outer layer (figs. 6, 7). Be-

tween any two adjacent angles, a single vascular bundle is found. Immediately inside of this is a broad band of parenchyma cells 0.3 mm. thick, essentially like the first except that the cell cavity contains a dense mucilaginous or resinous substance which makes it



FIG. 6.—*Trigonocarpon pusillus*: longitudinal oblique section showing three layers of integument; *sa*, sarcotesta with epidermis (*cp*); *m*, mucilage canal; *pa* parenchyma with dense cell contents, coaly layer; *sc*, sclerotesta; *n*, wrinkled nucellus; *mg*, megaspore membrane; *g*, gametophyte remains. H 214; $\times 10$.

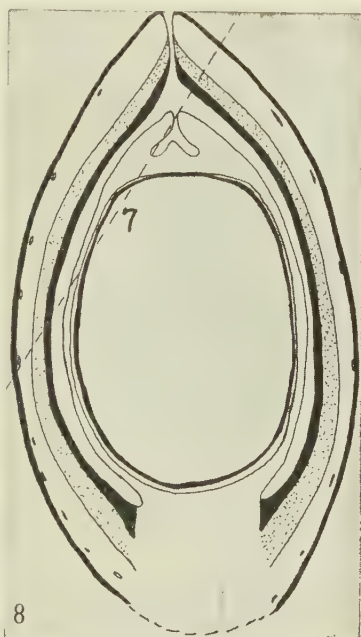
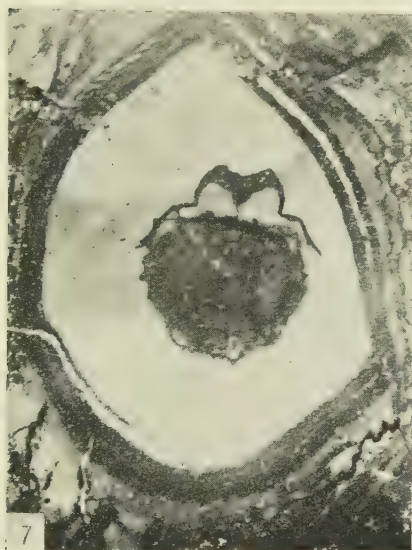
appear in the petrification as a coaly layer. Within this is the third layer, 0.2 mm. thick, of cells thickened as typical stone cells. In mass these latter two layers appear as a single one, although in places they are often separated through pressure (fig. 7).

The nucellus, greatly wrinkled in the basal portion, consists of a definite epidermal layer of cells elongated in a longitudinal direction, with less distinct cellular tissue within. Its only connection with the integument lies in the chalazal disk at the base. In sections nearly longitudinal (fig. 6) the megaspore membrane shows up in striking contrast to the nucellus, the former being a dense, opaque orange when etched with hydrochloric acid; the latter a clear amber. At the micropylar end the nucellus shows a centrally placed pollen chamber (fig. 7).

The matrix in which this seedlike structure was imbedded was so heterogeneous that it is a little hazardous to connect it with any given plant. Cordaites leaves were present as well as good speci-

mens of Medullosean petioles, *Sphenophyllum*, and stigmarian roots.

Trigonocarpon parkinsoni Brongniart.—This seed, the largest found in the Harrisburg material, is an elongated ovoid body 3-4 cm. in length and 2-2.5 cm. in width. In cross-section in the early stages it is roughly circular in outline, while later the twelve longitudinal ribs of the middle integument layer give it a sharply ridged contour. Of these ribs, the three

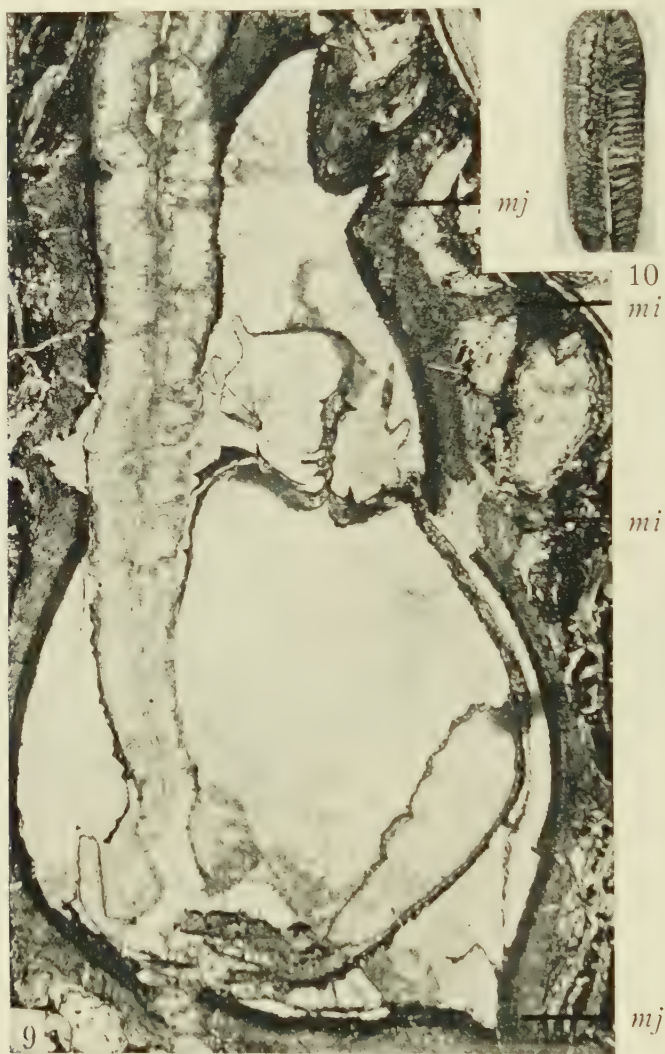


FIGS. 7, 8.—*T. pusillus*: section near micropyle showing pollen chamber of nucellus in addition to these features. H 214; $\times 10$. Fig. 8, reconstruction of median longitudinal section of *T. pusillus* from Harrisburg material; $\times 7$.

more prominent are the major and the nine less prominent are the minor ribs. They are arranged in a definite sequence, with three minor ribs lying between any two adjacent major ribs (fig. 9).

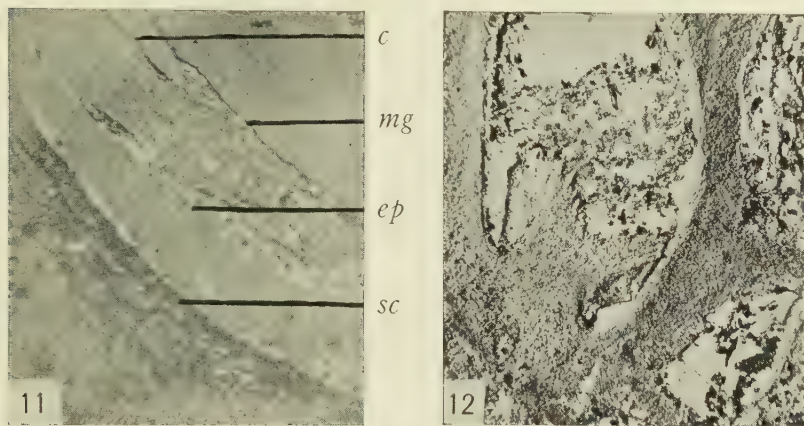
Two specimens formed the basis of study, and since they showed somewhat different stages of development, they give a clue to the progressive changes taking place in the maturation of the seed coat and the breakdown of the nucellus. At first glance the shape of the seed is suggestive of the *Platyspermeae*, but closer observation shows

this to be the result of lateral compression during fossilization. This process has not interfered with the excellent preservation of the cellular structure. The integument shows early differentiation into



FIGS. 9, 10.—Fig. 9, *Trigonocarpus parkinsoni*: cross-section from older seed showing *mj*, major ribs with minor ribs (*mi*) between. H 213; $\times 5$. Fig. 10, leaf of *Medullosa* (*Alethopteris*) taken parallel to surface, showing venation. H 213; $\times 10$.

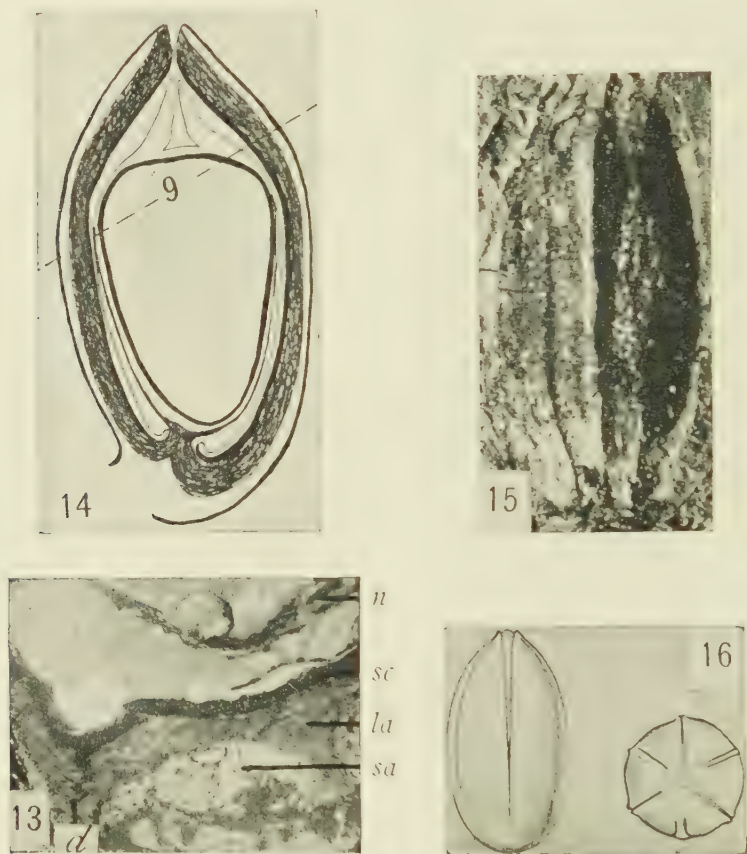
three layers of tissue: the outer, sarcotesta; the middle, lacunar sclerotesta; and the inner, compact sclerotesta. The parenchymatous sarcotesta, less than 1 mm. in thickness, is bounded externally by the small epidermal cells and several rows of thickened hypoderm. In this region lie the six vascular bundles which supply the integument. The inner margin of the sarcotesta merges gradually into a wider layer of lacunar tissue, sclerotesta, which makes up the



FIGS. 11, 12.—Details of nucellus and integument of *T. parkinsoni*: fig. 11, from younger seed showing undifferentiated outer layer of integument; *sc*, sclerotesta already differentiated; nucellus shown with epidermis (*ep*); *c*, conductive tissue of nucellus; *mg*, megaspore membrane. H 213; $\times 15$. Fig. 12, same, taken through chalaza. H 213; $\times 10$.

framework of the ribs. In median cross-section this layer is 2 mm. in thickness, extending out for 4 mm. in the region of the major ribs. In the later stage it is composed of cells, sinuous and irregular in shape, although in the earlier stage, as shown in fig. 11, the cells are isodiametric. The major ribs in the upper third of their length show a marked development of enlarged, thickened, intracostal cells (fig. 13) which mark the line of dehiscence of the seed in germination. An interesting correlation exists in the development of the integument layers and the structure of the nucellus. In the seed in which the integument appears to be in a younger condition, judging from the size and maturity of the cells, the nucellus is massive with a distinct epidermis, and has 8–12 conductive strands which

extend from the basal disk of sclerotic tissue up to the floor of the pollen chamber. The megaspore membrane is evident, tightly adhering to the inner wall of the nucellus. In the older, judging from



FIGS. 13-16.—Fig. 13, cross-section of major rib of older seed showing three layers of integument; *sa*, sarcotesta; *la*, lacunar sclerotesta; *sc*, sclerotesta; *d*, enlarged thickened intracostal cells marking line of dehiscence of seed during germination; *n*, nucellar remains. H 213; $\times 10$. Fig. 14, reconstruction of *T. parkinsoni* from Harrisburg material (median longitudinal section). $\times 2$. Fig. 15, cast of *Trigonocarpon* after NOÉ; about natural size. Fig. 16, cast of *Trigonocarpon* after ZEILLER, showing infiltration through dehiscence slit; about natural size.

its more mature middle integument layer and dehiscence slits, the nucellus is more wrinkled and thinner, in some places only the epi-

dermis being left. The megaspore membrane was not to be found. In comparison with the present day seeds, this has striking resemblance to one from which the embryo has germinated, leaving only the remains of the nucellus within the seed coat.

These seeds, both in size and structure, agree well with the *Trigonocarpon olivaeforme* described by WILLIAMSON (42), and later by WILD (41), who found them to have a longer micropyle than had been ascribed to them formerly. Later the same material, reinvestigated by SCOTT and MASLEN (37), was included under the species *T. parkinsoni*. While the present material lacks the elongated micropyle and sarcotestal "wing" reported by SCOTT and MASLEN, such a discrepancy could so easily be attributed to the preservation that I find no grounds for making a new species.

Reproductive organs described from casts by NOÉ (23) as *TripterospERMUM rostratum* Brongniart may represent casts of the external surface of such a *Trigonocarpon* with the sarcotesta removed or dried down in the process of fossilization. The nutlike internal casts of this species are among the most numerous fossils found in the Coal Measures.

The petrifications described here as *Trigonocarpon parkinsoni* were imbedded in a matrix of leaves and petioles of *Medullosa*. One of the leaves is shown in fig. 10. Since they represent the best preserved specimens found in any of the coal balls, it is supposed that they had not been carried far from the parent plant. Although no actual attachment of leaves or petioles to seeds has been found, the homogeneity of the matrix and certain structural likenesses strongly suggest that these reproductive organs belong to *Medullosa*.

Stephanospermum akenoides Brongniart.—The *Stephanospermum* found in the Harrisburg petrifications is much like that described from the English (24) and French (12, 13) coal balls. It is an elongated ellipsoid seed about 10 mm. in length and 5 mm. in greatest width. The crown of tissue which surrounds the micropyle rises for over a millimeter above the body of the seed (figs. 18, 19), and surrounds the micropyle, leaving a shallow perimicropylar trough less than 1 mm. in width. The testa consists of a double layer: the inner, 0.1 mm. thick, of longitudinally elongated cells which extend into the micropyle and form the core of the crown; and an outer wider

region 1 mm. thick of palisade-like cells with its long axis at right angles to the surface. Near the micropylar trough the micropyle appears slightly 6-angled, and sections near the base of the seed have somewhat the same appearance, while a median transverse section shows it to be almost circular in outline. The nucellus is poorly preserved (figs. 19, 20). Although much wrinkled and plasmolyzed, longitudinally elongated epidermal cells could be distin-



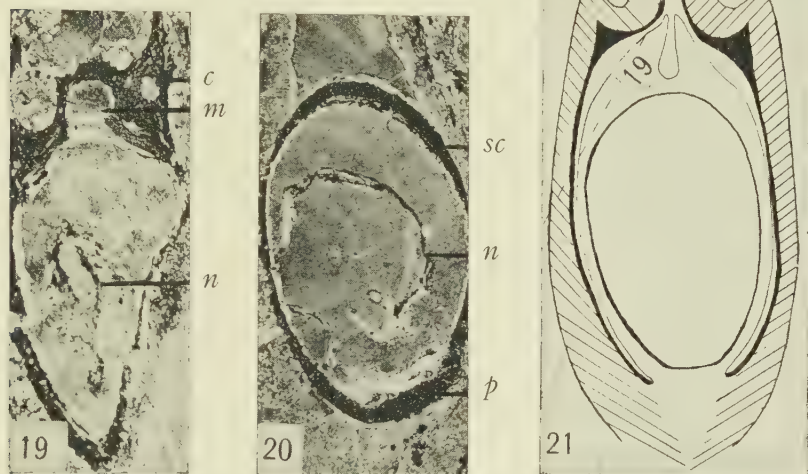
FIGS. 17, 18.—FIG. 17, impressions of sclerotesta and nucellus from seed remains of *Trigonocarpus*, after NEWBERRY. FIG. 18, longitudinal oblique section of *Stephanospermum akenoides* showing *m*, micropyle; *c*, crown of integument surrounding micropyle; *p*, palisade layer of integument; *sc*, sclerotesta; *n*, nucellar remains. H 215; $\times 10$.

guished, within which the megaspore membrane lay. No clue to the identification of the parent plant has as yet been discovered in the petrifications. Casts may be among those designated as *Rhabdocarpus*.

Morphological interpretation of seeds

Somewhat arbitrarily, perhaps, the term seed has been used in the foregoing descriptions rather than the terms fruit and nut of the earlier writers. According to the present day conception, a fruit is the seed-bearing product of the plant. This may consist of only the ovary or part of the ovary, or it may consist of other accessory parts

such as leaves (sporophylls), bracts, receptacle, etc. A nut is a type of fruit "hard indehiscent, 1-celled and 1-seeded" (16). From the descriptions it is evident that, with the possible exception of *Lepidocarpon*, an ovule with its single integument matured into several layers is all that is involved in the final structure. For this reason the term seed has superseded the terms fruit and nut in recent literature. A further question, however, presents itself as to the stage of development of these seeds: Are they true seeds in which



FIGS. 19-21.—Figs. 19, 20, longitudinal oblique sections of *Stephanospermum akenoides* (see legend for fig. 18 for details). $\times 10$. Fig. 21, reconstruction of median longitudinal section through *S. akenoides* from Harrisburg material. $\times 7$.

the embryo has not been preserved, as believed by BRONGNIART and RENAULT, or are they the younger stage known as the ovule?

In ontogeny the development of a seed is a dynamic process, beginning with the early growth of a nucellar mass, and passing into the stage of an integumented nucellus, within which the megaspore mother cell is differentiated. Up to this time the cells are meristematic, and may be said to be in a free, independent state. Beginning with the megaspore, accompanied sooner or later by development of the gametophyte structure, there is found a state of dependence of certain cells or groups of cells upon others. The first instance of this

is in the enlargement of the megaspore, when the tissues of the nucellus adjacent to the megaspore membrane are crushed and their contents assimilated by the developing megagametophyte. Later this is carried still further, in the dependence of the sporophyte upon the food material stored in the megagametophyte. In the early stages up to fertilization, such a structure is known as an ovule, and later as a seed.

When we think of the special care which must be taken in gathering material in the young stages of the present day plants for critical study of the reproductive organs, it is not surprising that embryo material is not found among the meager representatives which have been handed down from the abundant gymnosperm flora of the Paleozoic period. The chances are exceedingly small that such young tissue would break away from the parent plant, and it is only such material as might have undergone normal abscission that is ordinarily preserved. To pass to the other end of the life cycle, which is in the ordinary conception of the seed the most important; the greater part of the life cycle is concerned with the nourishing of the embryonic sporophyte. But in not a single seed found from the Paleozoic has there been any evidence of an embryo. Numbers cannot account for this, for in all the studies that have been made of some hundreds of specimens, none has given the slightest evidence of any stage of an embryo. A certain uniformity of structure prevails throughout. All seem to have been derived from orthotropous ovules. The integument may be diverged early (*Conostoma*) or late (*Trigonocarpon*), but in either case the cells constituting it reach maturity early, as is reported for living gymnosperm seeds. The integument differentiates into two and sometimes three integrading zones: the outer, sarcotesta, usually rather poorly preserved; the inner, sclerotesta, composed of compact fibrous tissues, usually much thickened as stone cells. In the earlier stages the nucellus is a rather massive structure, with definite epidermis of cells rounded in cross-section, somewhat elongated longitudinally, and with densely colored cell contents. It is always more or less wrinkled into deep folds as in a much plasmolyzed state. In its turgid condition it probably entirely filled the testal cavity, taking its contour from the pressure of the inner margin of the sclerotesta. The upper portion of the

nucellus was differentiated into a beaklike chamber in which pollen is sometimes found (3, 27). Within the nucellus the megaspore membrane is usually still present, closely following its inner margin. Gametophyte tissue is not as well preserved in the present material as in some of the English specimens (21), but is represented by a brownish mass of crystalline material occupying the center of the megaspore (10). The whole suggests a poorly preserved ovule of the cycad type, with a megagametophyte in a starchy gelatinous mass, just after the delicate cell walls have begun to come in.

Where the nucellar pollen chamber shows little breakdown of tissue, this structure should be interpreted as an ovule, perhaps abortive, perhaps only a normal stage in the life cycle which did not develop further because of the unfavorable conditions under which it happened to fall during the infiltration process. Some, with a thinner nucellar membrane, a beaklike projection of the nucellus into the micropyle, and a sclerotesta which shows the longitudinal splitting of the stony layer into valves with little or no sarcotesta left, represent a later stage in the ontogeny of the seed, where the embryo has escaped, leaving only the shell of the integument and nucellus behind. Such remains are found abundantly as casts (fig. 15 *a, b*). These, since they are of a much later stage but yet are indicative of their early seedlike nature, might best be designated as seed remains. With the earlier and later stages thus preserved, it is conceivable that we may yet find a seed, in the strictest sense of the term, with an embryo preserved, if a sufficient number of specimens in the form of petrifications, casts, and impressions are carefully observed.

Environmental theory for correlation of casts and impressions with petrifications

While it is not always safe to assume that similar appearances constitute a basis for relationship, it has been generally recognized (2) that, in the case of *Trigonocarpon* at least, a number of fossils produced by various forms of fossilization have been discovered to be so nearly alike as to be given the same species name. The method of preservation of each of these forms has been explained, but no adequate theory has been proposed to account for their correlation.

From the study of the morphology of such material as was available, a suggested theory, based upon ecological factors, has been formulated and will briefly be outlined.

All the ovules and seed remains show a constant, clearly defined abscission from the parent stalk which bore them. The integumental covering matured early, differentiating while it was still attached to the parent plant, even carrying the beginnings of the dehiscent mechanism. It is assumed that these seed-bearing plants, growing at or near the margin of the swampy arm of the sea, carried a hereditary factor for dropping the ovules early in their life history, at or near the time for pollination. Some of these, pollinated or unpollinated, fell into the deeper, still, brackish water. Further development of the ovule and subsequent germination were thus prevented. The nucellus was badly wrinkled through the plasmolyzing action of the brackish water, although the cells making up the whole were usually well preserved, free from bacterial action. These, imbedded in the organic remains making up the coal seam, are usually found in the coal balls (petrifications of coal seams). Sometimes such ovules fell on the muddy surface of the soil near the base of the plant, and their impressions were preserved, without the sarcotesta. In other cases pollination had been completed and an embryo formed which had germinated and escaped. Only the seed remains were left, often seen as valves (two in the case of *Cardiocarpon*, three in *Trigonocarpon*). The nucellus may be left as a thin papery layer not greatly wrinkled. It is through the micropylar opening that the sand and clay entered and formed such characteristic casts as those shown in fig. 15. It was the micropylar end of the nucellus, or possibly even a structure corresponding to the coleorhiza of the present-day cycads, that NEWBERRY saw and described as the 6-rayed star, the remains of the floral parts. These remains are now found as casts in the roof nodules of the coal seams or as impressions in the shale deposits formed by the sediments which flooded the gradually subsiding Coal Age swamps.

Summary

1. Certain rounded, flattened, or angular seedlike objects appearing as casts or impressions in the shale above the coal seams of the

Pennsylvanian in America have been designated as fruits, nuts, or seeds, in spite of the absence of structure-showing material. Such fructifications offering structure are now at hand from coal balls from coal no. 5, O'Gara Mine, Harrisburg, Illinois. Using the older method of thin rock sections and the newer one of KOOPMANS-WALTON, serial sections were obtained which formed the basis of a morphological study of the following species:

a. *Lepidocarpon lomaxi* Scott.—An elongated sporangium borne on the adaxial surface of the leaf (sporophyll), the outgrowing edges of which close up around the sporangium to form the integument; length 10 mm.; width of distal end 5 mm., proximal end 2 mm.; height 5–8 mm.; definitely identified as the fruiting structure of a *Lepidodendron*.

b. *Conostoma oblongum* Williamson.—An ellipsoid integumented ovule, 5 mm. $\times$ 2 mm.; integument of two layers: outer, palisade; inner, longitudinally elongated sclerenchyma; integument and nucellus undiverged as in modern cycads; lagenostome very small.

c. *Trigonocarpon pusillus* Brongniart.—A 3-angled ovule 12 mm. $\times$ 6 mm.; integument of three layers: outer, parenchymatous sarcotesta with numerous mucilage or resin canals, bounded externally by thick-walled epidermal cells; middle, parenchymatous, with dense cell contents; inner, sclerotesta or stony layer; relationship indefinite.

d. *Trigonocarpon parkinsoni* Brongniart.—Large seedlike structure, ovoid with 12 ribs; integument thick, differentiated into three layers: outer, parenchymatous sarcotesta, bounded by heavy-walled epidermis; middle, lacunar tissue making up the ribs; inner, sclerotesta, of cells longitudinally elongated; three major ribs show distinctly thickened intracostal dehiscence tissue in the upper one-third of their length. Nucellus similar to that found in *Pachyteta*, massive with sclerenchymatous chalazal disk, 8–12 conductive strands running longitudinally; and an outer densely colored epidermis. Casts of such seed remains are numerous throughout the coal seams.

e. *Stephanospermum akenoides* Brongniart.—An elongated ellipsoid ovule, 10 mm. $\times$ 5 mm., with conspicuous crown of tissue about the micropylar end; slightly 6-angled; integument of two layers:

outer, multiple palisade; inner, longitudinally elongated sclerenchyma.

2. With the exception of *Lepidocarpon*, these forms represent the remains of orthotropous ovules, unattached to the plants which bore them, although the matrix of leaves and stems in which they were found may give some clue as to the parent plant. The nucellus is always plasmolyzed as in poorly fixed tissue for histological study. It may consist of only a single layer of cells or of a multicellular layer showing some differentiation (epidermis, conductive tissue, parenchyma). No embryos were found, and often only traces of the megagametophytes were present. This cannot be owing entirely to the delicacy of such tissues, since bud tissue and even distinctly meristematic tissue are often found in other parts of the plant remains. It is presumed that those ovules with pollen chambers intact represent an early or middle stage in the development of the ovule. Others (where the nucellus is only a thin papery layer and the pollen chamber an elongated broken beak) probably represent the discarded seed coat after the embryo has been discharged in the normal process of germination. Certain impressions of *Trigonocarpon* from Ohio seem to suggest such a stage. Where a younger stage may be definitely recognized, the petrification may more accurately be referred to as an ovule; where it cannot be determined with certainty, "seed remains" is more accurate than fruit or nut.

3. An environmental theory, emphasizing the conditions under which each was fossilized, is proposed to account for the close relationship between the casts found in the shales above the coal seams and the petrified ovules of the coal balls imbedded in the coal layers.

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